



Integration of an Individual-Based Fish Bioenergetics Model into a Spatially Explicit Water Quality Model (CE-QUAL-ICM)

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PURPOSE: This technical note presents the results of incorporating a fish bioenergetics module into CE-QUAL-ICM, a spatially explicit eutrophication model. In addition to fish consumption of algae, zooplankton, and detritus, fish biomass accumulation and recycling to the water column are explicitly accounted for. Schools of fish are tracked individually, allowing for spatial resolution of their effects on phytoplankton and nutrient loading. These developments allow for investigations of the impact of planktivorous fish on water quality through consumption of algae and nutrient export via mass sequestering during growth. The formulation details of the new model system are outlined in this technical note.

BACKGROUND: As early as the 1960's-70's intense eutrophication events have occurred in sensitive estuaries, with increasing anthropogenic sources of nitrogen (N) and phosphorus (P) leading to excessive algal growth, degradation of water quality, and a general decline in ecological health. Most prior attempts to address estuarine eutrophication have focused on reducing nutrient loads; however, cost and difficulty in implementation have limited the effectiveness of such an approach. An alternate approach under consideration is the revitalization of primary consumers, including planktivorous fish, which can potentially reduce the quantity of algae and remove nutrients from estuarine systems via sequestering during growth. The model formulation presented in this technical note is designed to provide a way to quantify the potential impact managing planktivorous fish may have on the water quality of an ecosystem. A fish bioenergetics module based on the Wisconsin fish model (Hanson et al. 1997) was coupled into the spatially and temporally explicit water quality model, CE-QUAL-ICM. Fish are modeled as individual schools, allowing spatial and temporal resolution of water quality effects, and nutrient feedback through egestion, excretion, and mortality is explicitly modeled.

EUTROPHICATION MODEL: CE-QUAL-ICM is a three-dimensional eutrophication model that operates by enforcing conservation of mass on a set of state variables in each cell of a model grid. The state variables each belong to a set of categories that may be described as physical variables (salinity, temperature, etc.) and those in elemental cycles including carbon, nitrogen, phosphorus, silica, and oxygen (Cerco and Noel 2005; Cerco and Cole 1993). In the current formulation, active constituents are temperature, salinity, fixed inorganic suspended solids, three algal groups (nominally representing blue-green algae, spring diatoms, and green algae), two zooplankton groups (representing micro- and mesozooplankton), ammonium, oxidized nitrogen (nitrite/nitrate), dissolved oxygen, and various labile and refractory forms of dissolved and particulate carbon, nitrogen, phosphorus, and silica. Sources to the model are meteorological inputs and loading sources simulating riverine input; these sources are time-variant to capture the

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seasonal shifts in nutrient loading. The full details of the CE-QUAL-ICM model formulation may be found elsewhere (Cerco and Cole 1993; Cerco and Noel 2005).

FISH POPULATION DYNAMICS: Within CE-QUAL-ICM, fish are modeled as discrete “super-individuals,” representative of groups of individuals moving throughout the model grid. Parameters governing fish physiology are prescribed by “class,” which may represent a specific age, size, or other sub-group of fish. Hereafter super-individuals will be referred to as “schools,” noting that the difference between a super-individual and an actual school is the more diverse nature of the latter. A school may either be totally uniform in nature, consisting of a single class of fish, or it may consist of fractional components of multiple classes, each represented by an individual whose physical characteristics (length, weight, composition, etc.) are identical to all those members within the school of the same class.

Fish movement is governed by an external control file which prescribes the initial number of fish in a school, the fractional division between classes, and the cell location at any given point in time. This file is generated externally, and may either be done manually or through the use of algorithms to approximate fish migration with time.

Fish mortality within a school is accounted for within the model (variables used in all equations are listed in Appendix A):

$$\Delta N = \Delta N_{stv} + \Delta N_{suf} + \Delta N_{prd} + \Delta N_{fsh} \quad (1)$$

The total number of individuals lost (ΔN) within a time-step (Δt) is the sum of the number lost due to starvation (ΔN_{stv}) and suffocation (ΔN_{suf}), accounted for explicitly as functions of fish condition and model environment at any given time-step, along with the number lost to other natural causes (ΔN_{prd} , typically predation) and those caught by the fishery (ΔN_{fsh}). The number lost due to any specific process is a function of the mortality rate for that process, e.g. for starvation:

$$\Delta N_{stv} = N_t \cdot M_{stv} \cdot \Delta t \quad (2)$$

M is mortality (fish/s) and N_t is the number of individuals (fish) within a given school. Starvation and suffocation were accounted for based on models developed for Chesapeake Bay anchovy (Adamack 2007). If the wet weight of the representative individual for a school drops below 70 percent of the ‘healthy’ weight for that individual’s length, a daily mortality rate of 0.1 fish/day is introduced (converted to instantaneous mortality rate in fish/s as $M_{stv} = DFST / (24 \cdot 60 \cdot 60)$, where DFST is the daily mortality rate). ‘Healthy’ wet weight (WW, in g) is calculated from empirically determined length (L, in mm) to weight relationships, specific to fish species, and is presently formulated as:

$$WW_{ind, healthy} = AL \cdot L^{BL} \quad (3)$$

where AL and BL are empirically determined parameters. Suffocation mortality is calculated as (Adamack 2007):

$$DFSU = 0.093487 + 70.11894 \cdot (\ln[DO_{cell}])^2 \quad \text{if } [DO_{cell}] \leq 1 \text{ mg/l} \\ = 0 \quad \text{if } [DO_{cell}] > 1 \text{ mg/l} \quad (4)$$

$[DO_{cell}]$ is the concentration of dissolved oxygen (mg/l). Predation and fishing mortality are taken from values reported in the literature.

FISH BIOENERGETICS MODEL: Bioenergetics models rely on conservation principles, with the amount of energy a fish can devote to growth being the difference between consumption in the form of food and the sum of life process expenditures, including respiration, specific dynamic action, egestion, and excretion. The rate of wet weight growth can be calculated as:

$$\frac{\partial WW}{\partial t} = \left\{ C' - [(R' + S') + (F' + U')] \right\} \cdot \frac{1}{E_{pred}} \quad (5)$$

$\partial WW/\partial t$ is the rate of wet weight growth (g/s); E_{pred} is the energy density of the fish (J/g). The use of the prime symbol denotes these are rates of energy uptake of consumption (C'), respiration (R'), specific dynamic action (S'), egestion (F'), and excretion (U'), as opposed to a total quantity. Fish energy density is calculated as a linear function of representative individual weight:

$$E_{pred,t} = EPRD \cdot WW_{ind,t} \quad (6)$$

EPRD is an empirically determined predator energy density, variant by species. Growth in weight can subsequently be converted to growth in length via the aforementioned empirical length/weight relationship, noting that fish cannot shrink. At each time-step, the length of a school's representative individual is calculated from its new weight and compared to its length at the previous time-step; if the new length is greater than the old, the fish grows to this value, but if not, the fish retains its prior length and begins to have a weight deficit that could potentially lead to starvation mortality as previously described.

Consumption is based on a foraging model modified from one developed for Chesapeake Bay menhaden (Luo et al. 2001). Presuming the number of fish within a cell relative to the cell volume and length of time-step is not a limiting factor, each individual within a school has a volumetric clearing rate:

$$V'_s = f(DO) \cdot gap(L) \cdot u(T, L) \cdot eff(L) \quad (7)$$

V'_s is the volumetric clearing rate (m^3/s) and is based on the mouth gap area (gap, in m^2), swimming speed (u , in m/s), an empirically derived function of dissolved oxygen concentration within the cell the school occupies ($f(DO)$), and filtration efficiency ($eff(L)$, unitless). The dependence on dissolved oxygen is based on physiological fish response to stress (Luo et al. 2001):

$$f(DO) = \frac{1}{1 + \exp(-2.1972 \cdot [DO] + 6.5916)} \quad (8)$$

[DO] is the concentration of dissolved oxygen (mg/l). The mouth gap area is a function of body length (Luo et al. 2001):

$$\text{gap}(L) = 0.2586e - 5 \cdot (L)^{1.79767} \quad (9)$$

Swimming speed in some filter feeding species is a function of body length and food concentration, with fish exhibiting one characteristic swimming rate (in body lengths/s) when chlorophyll concentration exceeds a threshold to trigger ‘feeding’ behavior and a second, slower rate when chlorophyll does not exceed this threshold (Durbin and Durbin 1975). In the present formulation, based on observations of Atlantic menhaden, swimming velocity is calculated as:

$$\begin{aligned} u &= VELF \cdot \frac{L}{1000} \quad \text{if } \text{Con}_{\text{CHL}} > \text{FTHR} \\ &= VELNF \cdot \frac{L}{1000} \quad \text{if } \text{Con}_{\text{CHL}} < \text{FTHR} \end{aligned} \quad (10)$$

VELF and VELNF are the swimming velocities when feeding and non-feeding, respectively (fish body length/s), Con_{CHL} is the concentration of chlorophyll (g/m³), and FTHR is the feeding threshold (in g/m³). Modification would be necessary when applied to a species with a different observed behavior. Swimming velocity is consistent with the migration velocity used in tracking school location in that a school cannot migrate an unreasonably large distance compared to typical menhaden swimming velocities, but the two are not directly coupled. A direct link is not required since migration velocity captures directionally specified movement on relatively large temporal and spatial scales (hours and km), whereas moment-to-moment fish swim velocity and direction on the scale of the water quality time-step (minutes) may be much more sporadic.

Filtration retention efficiency may also be a function of fish length. In the current formulation, the relationship is a sigmoid response curve developed for Atlantic menhaden (Luo et al. 2001):

$$\text{eff}(L) = \frac{0.5}{(1 + \exp(-0.0527811 \cdot L + 2.96973))} \quad (11)$$

In formulations with application to other species of fish, modification of this empirically determined relationship may be required.

Within the model cells, it is possible that the volumetric clearing rate by schools will need to be limited so that the volume filtered within the time-step does not exceed the cell volume. In this case, the fraction of potential volumetric clearing rate by an individual is compared to the total volumetric clearing rate of all individuals within the cell. This value is multiplied by the volumetric clearing rate to turn over the entire cell during a time-step to determine the maximum clearing rate for that individual. Fish mortality is accounted for prior to feeding, therefore the number of individuals in a school is the value at the end of the time-step:

$$V'_{s,\max} = \frac{\Delta V}{\Delta t} \cdot \left[\frac{V'_s}{\sum(N_{s,t+\Delta t} \cdot V'_s)} \right] \quad (12)$$

In this equation ΔV is the total cell volume (m^3); Δt is the length of the time-step (s); V'_s is the volumetric clearing rate of an individual within the school as defined previously; and $N_{s,t+\Delta t}$ is the number of individuals at that end of the time-step (e.g., after mortality). If the combination of fish population, cell size, and model time-step are such that this alternative calculation is widely employed, growth or oxygen intake will become unrealistically restricted, and the grid cell size or the time-step will need to be modified.

Energy consumption is a function of volumetric clearing rate, filtration efficiency, and the energy concentration within the grid cell, calculated from the mass density of food sources and their energy density. Model fish consume food at all times, causing unrealistically large overall growth compared to biological fish, which only consume food during a portion of their waking hours. Therefore, a feeding fraction is introduced, which limits food consumption at all times to a fraction of possible total consumption. This feeding fraction is selected empirically to calibrate fish growth patterns to those observed in the field.

The three types of prey considered within the model are phytoplankton, mesozooplankton, and detritus. The total algal concentration is the sum of the three model algae species (Con_{phyto} , in gC/m^3); retention efficiency is independent of prey source in the model.

Detrital food sources are also considered. Detritus is handled by the model as individual elemental forms of particulate matter, the sum of which is taken as the dry weight of detritus:

$$Con_{det} = LPOC + RPOC + LPON + RPON + LPOP + RPOP + PS \quad (13)$$

Con_{det} is the total (dry) concentration of particulate constituents (g/m^3), including labile and refractory particulate organic carbon (LPOC and RPOC, in gC/m^3), labile and refractory particulate organic nitrogen (LPON and RPON, in gN/m^3), labile and refractory particulate organic phosphorus (LPOP and RPOP, in gP/m^3), and particulate silica (PS, in gSi/m^3). Concentration of wet weight of detritus is calculated assuming a dry weight to wet weight ratio of 0.2 (Rippetoe 1993), and a fixed energy density set in the control file is used to convert this wet weight concentration to energy concentration. These calculations yield a very approximate value of energy consumption from detrital sources for menhaden, given that actual detritus energy density has a complex dependence on composition that could not be captured using the model constituents (Tenore 1981).

Combining phytoplankton, zooplankton, and detrital food sources, the total rate of energy consumption becomes:

$$C' = FFRC \cdot \left(\frac{Con_{phyto}}{CtWP} \cdot EPLK + \frac{LZ}{CtWZ} \cdot EZOO + \frac{Con_{det}}{DWW_{det}} \cdot EDET \right) \cdot V'_s \quad (14)$$

FFRC is the aforementioned empirically determined feeding fraction (unitless). Algal model units are grams of carbon/ m^3 , but energy density values (EPLK) are in joules per gram of wet weight, therefore a conversion factor of carbon to wet weight ratio (CtWP, in gC/gWW) is required, and is taken as 0.1 (Peters and Downing 1984). Similarly for zooplankton,

$CtWZ = 0.04344$, based on a gDW/gWW ratio of 0.1086 (Durbin and Durbin 1998) and a gC/gDW ratio of 0.4.

Energy is lost due to physiological processes including respiration, specific dynamic action, excretion, and egestion, which are modeled using a methodology following the Wisconsin Fish Model (Hanson et al. 1997). Rate of energy loss to respiration is determined from mass consumption of oxygen. R'_O is calculated from physiological parameters specific for a given fish species, a temperature dependence function, and an activity multiplier.

$$R' = R'_O \cdot E_O \quad (15)$$

$$R'_O = RESA \cdot WW_t^{RESB} \cdot f(T) \cdot ACT \cdot \left(\frac{WW_t}{86400} \right) \quad (16)$$

R'_O is the rate of oxygen consumption (g/s); E_O is an oxycalorific coefficient (J/g O₂); RESA and RESB are the fish-specific physiological parameters on an annual basis; $f(T)$ is a temperature dependency function, and ACT is an activity multiplier. The temperature dependence of oxygen consumption is calculated as:

$$f(T) = V^X \cdot \exp(X \cdot (1 - V)) \quad (17)$$

$$V = (RTM - T) / (RTM - RTO) \quad (18)$$

$$X = \left(Z^2 \cdot \left(1 + (1 + 40/Y)^{0.5} \right)^2 \right) / 400 \quad (19)$$

$$Z = \ln(RQ) \cdot (RTM - RTO) \quad (20)$$

$$Y = \ln(RQ) \cdot (RTM - RTO + 2) \quad (21)$$

T is temperature (°C) and RQ, RTM, and RTO are fish-specific physiological parameters. Since swimming velocity depends on the chlorophyll-triggered feeding state, a similar behavior dependence is introduced into both the activity multiplier and the oxycalorific coefficient based on empirical observation, with E_O , feed = 13388.8 J/g O²; E_O , nonfeed = 13723.5 J/g O² (Durbin and Durbin 1983). Activity multipliers during both feeding and non-feeding states are set in the fish control file.

The bioenergetics model assumes unlimited oxygen availability, which may not be true. If oxygen is limiting (i.e., if the fish would consume more oxygen in a time-step than is present in the grid cell), the volumetric clearing rate previously calculated is used to determine the actual rate of oxygen mass consumption:

$$R_O = V'_{s,\max} \cdot [DO] \quad (22)$$

Egestion energy loss rate is calculated as a percentage of consumption, and excretion and specific dynamic action losses are calculated as a percentage of rate of energy assimilated (e.g., consumption minus egestion).

$$S' = SDA \cdot (C' - F') \quad (23)$$

$$F' = FA \cdot C' \quad (24)$$

$$U' = UA \cdot (C' - F') \quad (25)$$

SDA, FA, and UA are empirically determined, species-specific factors.

Fish Composition: Fish bioenergetics calculations are based on energy conservation, but within the model environment, constituent element mass (e.g., carbon, nitrogen, phosphorus, silica) must also be conserved. In the model, an empirical value of fish composition for each of the constituent elements was specified for each class, fixing the ideal fraction of each element as a function of total wet weight. Under certain environmental conditions, it is possible that consumption of an individual element relative to growth determined by energy consumption is insufficient to maintain this target fraction, therefore elasticity is allowed wherein a fish can incur an elemental deficit, and subsequently retain higher fractions of that element when it is in abundance to regain the target composition. The amount of a given element a fish needs to retain at each time-step is calculated as:

$$Need_E = WW_{t+\Delta t} \cdot DWWW \cdot FEDW - WW_t \cdot DWWW \cdot aFEDW_t \quad (26)$$

This amount ($Need_E$) is a function of the dry weight to wet weight ratio (DWWW, unitless), the wet weight before and after the time-step (WW, g), the target fraction of that element (FEDW, unitless), and the actual fraction of that element at the previous time-step (aFEDW_t, unitless). It should be emphasized that the elasticity in the model does not mimic realistic changes in fish composition; however, it allows for conservation of mass within the model and prevents unrealistic individual element consumption requirements from being imposed. Elemental composition could theoretically drop to unrealistically low levels, but such a deficit would indicate a problem with the parameterization of the model environment or the fish, as a real fish is still subject to elemental mass availability and conservation.

Coupling to Water Quality Model: To conserve mass on the model grid, prey constituent concentrations must decrease with consumption, and fish outputs due to respiration, egestion, and excretion must return to the water column. In addition, mass from fish that die of natural mortality should return in the grid.

For each algal group, a school's consumption rate is calculated from the volumetric clearing rate, the number of individuals in the school, and the original concentration:

$$\frac{\partial B_k}{\partial t} = -V'_s \cdot N_{t+\Delta t} \cdot B_k \quad (27)$$

B_k gives the concentration of algae group k (gC/m^3). Similarly for mesozooplankton:

$$\frac{\partial LZ}{\partial t} = -V_s' \cdot N_{t+\Delta t} \cdot LZ \quad (28)$$

LZ gives the concentration of mesozooplankton (gC/m^3). Conservation of other constituents is relatively more complicated, in that fish can either be solely producers (e.g., ammonium) or both consumers and producers (e.g., particulate matter). For each element considered within the model (carbon, nitrogen, phosphorus, silica), a recycling rate is calculated as the total rate at which the element is returned to the water column by the fish.

Carbon mass balance dictates the growth rate in carbon:

$$G'_c = C'_c - (R'_c + F'_c + U'_c) \quad (29)$$

G'_c is the growth rate in carbon (gC/s) and is a function of carbon uptake (C'_c , in gC/s), respiration (R'_c , in gC/s), egestion (F'_c , in gC/s), and excretion rates (U'_c , in gC/s). Carbon uptake is governed by fish consumption, a function of the actual volumetric filtering rate of the school and the original concentration of the carbon containing prey sources (algae, mesozooplankton, labile and refractory organic carbon):

$$C'_c = V_s' \cdot N_{t+\Delta t} \cdot \left(\sum_{k=1}^3 B_k + LZ + LPOC + RPOC \right) \quad (30)$$

Inorganic carbon is not explicitly accounted for in the model; however, the loss of carbon due to respiration must be considered. The rate of carbon emission due to respiration is calculated as:

$$R'_c = R'_o / AOCR \quad (31)$$

R'_c is the rate of carbon emission (gC/s) and is a function of the rate of oxygen consumption and the oxygen-to-carbon ratio in respiration (AOCR, in gO_2/gC). Using the same simple model for aerobic respiration as in the water quality model:



Respiration of 6 moles of dissolved oxygen produces 6 moles of carbon dioxide, which converts to an AOCR of $2.67 \text{ g O}_2 \text{ g}^{-1}\text{C}$.

The ideal carbon recycling rate (CRRATE, in $\text{gC}/\text{s/fish}$) is therefore:

$$CRRATE = F'_c + U'_c = C'_c - G'_c - R'_c = C'_c - Need_c - \left(\frac{R'_o}{AOCR} \right) \quad (33)$$

If the calculated recycling rate were to fall below zero, the fish would (unrealistically) absorb nutrients directly from the water column; therefore, the actual carbon recycling rate is calculated as:

$$CRRATE = \max \left[C_c - Need_c - \left(\frac{R_o}{AOCR} \right), 0 \right] \quad (34)$$

The total change of any non-particulate constituent j is calculated as:

$$\frac{\partial C_j}{\partial t} = \frac{N_{t+\Delta t} \cdot CRRATE \cdot FC_j F + N_t \cdot M_{nat} \cdot WW_t \cdot DWWW \cdot FCDW_t \cdot FC_j FM}{\Delta V} \quad (35)$$

The distribution of recycled carbon to a model constituent (denoted as ‘j’; e.g., refractory particulate organic carbon, labile dissolved organic carbon, etc.) by a living fish ($FC_j F$) is governed by fractions fixed as input parameters to the model. Note that fish consume/produce discrete masses of constituents, but constituent quantities are accounted for as volumetric concentrations. Additional carbon recycling occurs due to natural mortality (starvation, suffocation, and predation, the sum of which results in a total natural mortality rate, M_{nat}); in contrast, fishing mortality is a sink from the system. The distribution of recycled carbon from mortality is controlled by fractions input to the model ($FC_j FM$).

For particulate matter, losses to fish consumption are also included:

$$\frac{\partial C_j}{\partial t} = \frac{N_{t+\Delta t} \cdot CRRATE_f \cdot FC_j f + N_t \cdot M_{nat} \cdot WW_t \cdot DWWW \cdot FCDW_t \cdot FC_j f M - N_{t+\Delta t} \cdot V'_s \cdot [j]}{\Delta V} \quad (36)$$

In this equation, $[j]$ is the concentration of constituent j (in g/m^3). Note that fish die before they eat, therefore the “living” fish recycling rate is multiplied by the new population, whereas the recycling due to mortality is multiplied by the old population and mortality rate. The recycling fractions for a specific fish may be estimated, for example, from empirically determined values for that species or a similar one. The new fish carbon fraction is calculated from the actual consumption and recycling rates as:

$$FDCW_{t+\Delta t} = \frac{(WW_t \cdot DWWW \cdot FDCW_t + \Delta t \cdot (C_c - R_c - CRRATE_f))}{DWWW \cdot W_{t+\Delta t}} \quad (37)$$

For the nitrogen constituents, respiration is not a factor, therefore nitrogen growth rate is governed by:

$$G'_N = C'_N - (F'_N + U'_N) \quad (38)$$

Within the eutrophication model, algal/zooplankton nitrogen is accounted for as a fraction of each species’ carbon concentration. Nitrogen uptake is governed by this fixed ratio and the nitrogen in the particulate matter consumed:

$$C'_N = V'_s \cdot \left[\sum_{k=1}^3 (B_k \cdot A_{NC_k}) + LZ \cdot ANClz + [LPON] + [RPON] \right] \quad (39)$$

Anc_k is the algal nitrogen to carbon ratio (gN/gC); $ANClz$ is the zooplankton nitrogen to carbon ratio (gN/gC). Following the calculations for carbon, the required nitrogen intake to maintain/achieve the target composition is calculated as:

$$Need_N = WW_{t+\Delta t} \cdot DWWW \cdot TFNDW - WW_t \cdot DWWW \cdot FNDW_t \quad (40)$$

Nitrogen recycling to the water column is therefore:

$$NRRATEf = F'_N + U'_N = C'_N - G'_N = \max [C'_N - Need_N, 0] \quad (41)$$

And the rate of recycling of dissolved nitrogen becomes:

$$\frac{\partial N_j}{\partial t} = \frac{N_{t+\Delta t} \cdot NRRATEf \cdot FN_j f - N_t \cdot M_{nat} \cdot W_t \cdot DWWW \cdot FNDW_t \cdot FN_j f M}{\Delta V} \quad (42)$$

Whereas for particulate constituents the rate of change becomes:

$$\frac{\partial N_j}{\partial t} = \frac{N_{t+\Delta t} \cdot NRRATEf \cdot FN_j f + N_t \cdot M_{nat} \cdot WW_t \cdot DWWW \cdot FNDW_t \cdot FN_j f M - N_{t+\Delta t} \cdot V'_s [j]}{\Delta V} \quad (43)$$

The recycling fraction of nitrogen to each model constituent from egestion/excretion is again based on empirical observation. The new fish composition is calculated from consumption and recycling rates as:

$$FNDW_{t+\Delta t} = \frac{(W_t \cdot DWWW \cdot FNDW_t + \Delta t \cdot (C_N - R_c - NRRATE_f))}{DWWW \cdot W_{t+\Delta t}} \quad (44)$$

Calculations for phosphorus constituents are identical to those for nitrogen constituents.

The fraction of silica within fish is taken as zero, therefore all silica is recycled immediately to the two model constituents in a 50/50 split:

$$\frac{\partial DS}{\partial t} = \frac{FDSf}{\Delta V} \cdot N_{t+\Delta t} \cdot V'_s \cdot \left[\sum_{k=1}^3 (Asc_k \cdot B_k) + [PS] \right] \quad (45)$$

$$\frac{\partial PS}{\partial t} = \left\{ \frac{FDSf}{\Delta V} \cdot N_{t+\Delta t} \cdot \left[\sum_{k=1}^3 (Asc_k \cdot B_k) + [PS] \right] \right\} - N_{t+\Delta t} \cdot V'_s [PS] \quad (46)$$

[DS] and [PS] are the concentrations of dissolved and particulate silica, and the other variables within the equation follow the convention previously described for carbon, nitrogen, and phosphorus. Rate of change of concentration of dissolved oxygen is related to the mass of oxygen consumed per fish, the population, and the cell volume:

$$\frac{\partial DO}{\partial t} = -N_{t+\Delta t} \cdot \frac{R'_o}{\Delta V} \quad (47)$$

Several assumptions and simplifications are inherent to this estimate of nutrient recycling from the fish to the model environment. Both mortality and the life processes of respiration, egestion, and excretion are treated as instantaneous processes, with mass returning to the water column in the same time-step as death/food consumption. In addition, elemental mass state must be simplified to fit within the confines of the water quality model constituents.

MODEL IMPLEMENTATION: The fish bioenergetics module is turned on and off using a control card added to the water quality model control file, at present hard-wired to be named “wqm_con.npt” (Appendix B; note that only a portion of the water quality model is shown to illustrate the proper placement of the fish card).

A separate control file, “fbm_con.npt,” governs the implementation of the fish bioenergetics module (Appendix C). The first card is the TITLE card, and consists of six lines of text used to make notes regarding the model run (these lines do not impact actual code implementation).

The next control card, “JDO,” indicates the julian day offset of the fish migration in relation to the julian day within the model run. If the fish migration file is referenced to the same start time as the model run, this card should be set to zero. If the fish migration is referenced to some other point (for example, day 0 in the model corresponds to January 1, but day 0 in the migration pattern corresponds to the start of the spring fish run on March 1), the offset between the two should be inserted in days (for the prior example, March 1 = julian day 60, January 1 = julian day 1, therefore JDO = (60 – 1) = 59).

IFRC controls what fraction of the population in the migration file is actually run through the model. This card allows for comparison of the effects of differing numbers of populations, while maintaining an identical migration pattern. Similarly, FFRC governs the fraction of the fishing mortality (set in a separate card in the control file) to provide a convenient method to investigate the impact of varying this parameter.

NGRP dictates the number of groups/classes for which bioenergetics parameters are to be prescribed. IGWT and IGLN are the individual fish entry weight and length for each class; the number of columns should correspond to the number of groups given in NGRP. EPLK, EZOO, and EDET are the energy densities (in J/g of wet weight) of phytoplankton, zooplankton, and detritus, respectively.

The next set of cards governs the bioenergetics parameters for the fish themselves; once again, there should be a column for each group specified in NGRP. These variables have been previously described and are defined in the variable list, marked with an asterisk indicating they are control cards.

AFNM and AFFM are the instantaneous annual predation and fishing mortality rates (fish/year), respectively. The next sets of cards (COMPOSITION through S RECYC) govern various parameters of the subject fish species; these cards have also been previously described.

The TRKC card governs turning the fish output files on and off. Output files can be generated at varying time intervals (e.g., one output every 10 days, one output every 365 days, etc.); NTRK governs how many output files will be generated. TRKD governs the starting day for each of the output files, and TRKF the frequency (in julian days) to output to each file.

NITKF dictates the number of input fish movement files, which are listed in ITKFN; these are assumed to be in chronological order by the model.

TRKFN, MRTFN, BINFN, BNTFN, and BCONF govern the file names for the various fish output files.

Fish movement is controlled via fish migration input files (Appendix D) read into the model; names of the files are controlled with the ITKFN card in the fish control file.

The first line of the migration input file allows the user to input information regarding the run, and is not used by the model. The migratory period indicates at what time the model should move to the next fish control file (if one exists). The user should ensure that the end time of the last migratory file is later than the end of the model run to prevent unpredictable behavior if the model attempts to move past the end of the last input file.

The rest of the file dictates the location of a school at any given point in time. At each time-step, the number of schools is the total number undergoing movement at that time-step; any school not explicitly listed is assumed to occupy the same model cell as it did when last specified. For example, school 1 enters the grid in cell 72 at time 0.00, and is assumed to remain in cell 72 until time-step 0.50, when it moves again. Any school that does not exit before the end of the migratory period is assumed to remain on the model grid; users should take care to ensure all schools either exit the grid before the end of the input file, or that their movement is specified in subsequent input files. The “size” of each school is the initial population; actual population at any given point in time is governed by mortality within the model. The group ID corresponds to the class number within the fish control file governing the bioenergetics parameters.

ADDITIONAL INFORMATION: For additional information, contact Dr. P. Soupy Dalyander (601-634-4612, Patricia.A.Dalyander@usace.army.mil) or Dr. Carl F. Cerco (601-634-4207, Carl.F.Cerco@usace.army.mil). This research was funded through the System-Wide Water Resources Program (SWWRP); for more information on SWWRP, please visit <https://swwrp.usace.army.mil>, or contact the Program Manager, Dr. Steven L. Ashby (Steven.L.Ashby@usace.army.mil).

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APPENDIX A: Variables: Variables marked with an asterisk are cards in the fish control file.

*ACTF	= activity multiplier during feeding times (unitless)
*ACTNF	= activity multiplier during non-feeding times (unitless)
*AL	= empirical fish coefficient for determining length/weight relation (units may vary)
AOCR	= oxygen-to-carbon ratio in respiration (gO ₂ /gC)
B _k	= concentration of algal group <i>k</i> (gC/m ³)
*BL	= empirical fish coefficient for determining length/weight relation (units may vary)
C'	= rate of energy consumption (J/s)
<i>C'</i> _E	= consumption rate of element <i>E</i> (gE/s)
Con _{det}	= concentration of detritus (g/m ³)
Con _{CHL}	= concentration of chlorophyll (mg/l)
Con _{phyto}	= concentration of phytoplankton (gC/m ³)
CtWP	= ratio of carbon to wet weight of phytoplankton (gC/gWW)
CtWZ	= ratio of carbon to wet weight of zooplankton (gC/gWW)
[DO]	= concentration of dissolved oxygen (mg/l)
*DWWW	= dry weight to wet weight ratio (unitless)
DWWW _{det}	= ratio of dry weight to wet weight of detritus (gDW/gWW)
E _{pred}	= energy density of the modeled fish (J/g)
E _O	= oxycalorific coefficient (J/g)
eff	= fish filtration efficiency (unitless)
*EDET	= energy density of detritus (J/g of wet weight)
*EPLK	= energy density of phytoplankton (J/g of wet weight)
*EPRD	= empirically determined predator energy density (units may vary)
ERRATE	= recycling rate of element <i>E</i> (g/s)
*EZOO	= energy density of zooplankton (J/g of wet weight)
F'	= rate of energy loss of egestion (J/s)
<i>F'</i> _C	= egestion rate of element <i>E</i> (gE/s)
*FFRC	= fish feeding fraction (unitless)
*FTHR	= chlorophyll threshold for fish to swim at “feeding” speed (g/m ³)
*FA	= empirical coefficient of egestion (unitless)

$*FEDW$	= fraction of element E in ideal fish composition, e.g., FCDW would denote fraction of carbon (gE/gDW)
$*FMCF$	= recycling of model constituent MC in elemental cycle E as a fraction of ERRATE from a living fish (e.g., fraction of recycled carbon, CRRATE, recycled to labile dissolved organic carbon is denoted FLDOCF)
$*MCFM$	= recycling of model constituent MC in elemental cycle E as a fraction of the total rate of mass of element E returned due to mortality (see FMCF)
$FSOE$	= concentration of an organic model constituent, where F is the form (labile or refractory), S is the state (particulate or dissolved), and E is the element (carbon, nitrogen, or phosphorus); e.g., RPOC is Refractory Particulate Organic Carbon, LDON is Labile Dissolved Organic Nitrogen, etc. (g/m ³)
G'_E	= growth rate of element E (gE/s)
gap	= fish mouth gap area (m ²)
L	= length (mm)
LZ	= concentration of mesozooplankton (gC/m ³)
M	= instantaneous mortality (fish/s)
N_t	= number of individuals at time t (# of fish)
$Need_E$	= amount of element E needed during a time-step to attain ideal composition (gE)
$*QR$	= empirical respiration coefficient (units may vary)
R'	= rate of energy loss to respiration (J/s)
R'_C	= respiration rate of carbon (gC/s)
R'_O	= rate of oxygen consumption (g/s)
$*RESA$	= empirical respiration coefficient (units may vary)
$*RESB$	= empirical respiration coefficient (units may vary)
$*RTM$	= empirical respiration coefficient (°C)
$*RTO$	= empirical respiration coefficient (°C)
S'	= rate of energy loss to specific dynamic action (J/s)
$*SDA$	= empirical coefficient of specific dynamic action (unitless)
T	= temperature (°C)
u	= fish swimming speed (m/s)
U'	= rate of energy loss to excretion (J/s)
U'_C	= excretion rate of element E (gE/s)
$*UA$	= empirical coefficient of excretion (unitless)

V'_s	= fish volumetric clearing rate (m^3/s)
VELNF	= fish swim velocity when not feeding (m/s)
VELF	= fish velocity when feeding (m/s)
WW	= wet weight (g)
ΔN	= number of individuals lost within a time-step (# of fish)
Δt	= length of a time-step (s)

APPENDIX B: Portion of a water quality control file, showing the addition of the card to implement the fish module.

Control file for WQM

```
TITLE C .....TITLE
Control file for 30-box model of Chesapeake Bay
Created Feb 23, 2005
Consistent with 2002 Chesapeake Bay model
Some modifications as per Patuxent model
These include fix-up to sed model CH4, alterations in mineralization
rates and alteration to algal nitrogen preference

GEOM DEFINE   NB      NSB      NQF      NHQF      NSHQF      NL
              4073     729      9874     6530      1251       15

TIME CON   TMSTRT   TMEND
          0.0      1095.0

# DLT      NDLT
          1

DLT DAY    DLTD     DLTD     DLTD     DLTD     DLTD     DLTD     DLTD     DLTD     DLTD
          0.0

DLT VAL    DLTVAL   DLTVAL   DLTVAL   DLTVAL   DLTVAL   DLTVAL   DLTVAL   DLTVAL   DLTVAL
          864.

DLT MAX    DLTMAX   DLTMAX   DLTMAX   DLTMAX   DLTMAX   DLTMAX   DLTMAX   DLTMAX   DLTMAX
          1000.0

DLT FTN    DLTFTN   DLTFTN   DLTFTN   DLTFTN   DLTFTN   DLTFTN   DLTFTN   DLTFTN   DLTFTN
          0.95

HM DLT    AHMDLT   FILGTH
          45000.0 364.583

-----
CONTROLS   SEDC     AUTOC    VBC      BFOC     STLC     ICIC     ICOC     SAVMC
          ON       ON       ON      ON       ON      BINARY   ON       ON
CONTROLS   SUSFDC   DEPFDC   LOXC     FISH     ON
          ON       ON       ON      ON       ON      ON      ON       ON
-----
-----  

ZFO FILE.....ZFOFN
outputs/wqm_zfo.test_050506

BFO FILE.....BFOFN
outputs/wqm_bfo.test_050506

SVO FILE.....BFOFN
outputs/wqm_svo.test_050506

AHY FILE.....AHYFN
outputs/wqm_aho.test_050506
```

APPENDIX C: Example of a fish control file.

Control file for Fish

TITLE CTITLE.....
 30 Box water quality model.
 Hacking menhaden with 30 box sediment transport.
 December 4, 2008
 Fish control file
 Extra comment line
 Extra comment line

JULIAN	JDO	IFRC	FFRC
	0.0	1.00	1.00
GRP PARA	NGRP		
	4		
INIT WT	IGWT	IGWT	IGWT
	1.00	85.6	167.1
			284.8
INIT LTH	IGLN	IGLN	IGLN
	48.0	202.0	252.0
			300.0
ENRGY DEN	EPLK	EZOO	EDET
	6020.	2790.	900.
BIOE PARA	EPRD	EPRD	EPRD
	3938.	8717.	8717.
	DWWW	DWWW	DWWW
	0.216	0.334	0.334
			0.334
	RESA	RESA	RESA
	3.301e-3	0.00294	0.0027
			0.003
	RESB	RESB	RESB
	-0.2246	-0.0085	-0.01
			-0.01
	RTO	RTO	RTO
	33.	33.	33.
			33.
	RTM	RTM	RTM
	36.	36.	36.
			36.
	QR	QR	QR
	2.07	2.5	2.5
			2.5
	SDA	SDA	SDA
	0.172	0.172	0.172
			0.172
	ACTF	ACTF	ACTF
	3.5	3.5	3.5
			3.5
	ACTNF	ACTNF	ACTNF
	1.0	1.0	1.0
			1.0

	FA 0.14	FA 0.14	FA 0.14	FA 0.14				
	UA 0.1	UA 0.1	UA 0.1	UA 0.1				
MORTALITY	AFNM 1.23	AFNM 0.72	AFNM 0.60	AFNM 0.55				
	AFFM 0.02	AFFM 0.22	AFFM 0.85	AFFM 1.37				
COMPOSITION	FCDW 0.566	FNDW 0.080	FPDW 0.024					
FSH PARA	GAPA 0.02586	GAPB 1.79767	SPDA 2.5	SPDB -0.398	SPDC 6.378			
	EFFA 0.5	EFFB -0.0527811	EFFC 2.96973	AL 7.1E-6	BL 3.07			
	VELF 1.67	VELNF 0.47	FTHR 0.004	FFRC 0.75				
C RECYC	FLDOCF 0.25	FRDOCF 0.0	FLPOCF 0.50	FRPOCF 0.25				
	FLDOC FM 0.25	FRDOC FM 0.0	FLPOC FM 0.50	FRPOC FM 0.25				
N RECYC	FNH4F 0.56	FUREAF 0.0	FLDONF 0.24	FRDONF 0.0	FLPONF 0.1	FRPONF 0.1		
	FNH4FM 0.55	FUREAFM 0.0	FLDONFM 0.2	FRDONFM 0.0	FLPONFM 0.2	FRPONFM 0.05		
P RECYC	FPO4F 0.5	FLDOPF 0.4	FRDOPF 0.0	FLPOPF 0.05	FRPOPF 0.05			
	FPO4FM 0.5	FLDOPFM 0.4	FRDOPFM 0.0	FLPOPFM 0.05	FRPOPFM 0.05			
S RECYC	FPSF 0.5	FDSF 0.5						
FSH RPRT	TRKC ON	NTRK 1						
FSH DAY	TRKD 0	TRKD	TRKD	TRKD	TRKD	TRKD	TRKD	TRKD
FSH FRQ	TRKF 1.0	TRKF	TRKF	TRKF	TRKF	TRKF	TRKF	TRKF
# FILES	NITKF 10							

INPUT TRACK FILES.....ITKFN.....
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt
merged_tracks.npt

OUTPUT SNAP TRACK FILE.....TRKFN.....
outputs/fsh_trk.opt

OUTPUT MORTALITY FILES.....MRTFN.....
outputs/fsh_mrt.opt

OUTPUT MASS BINARY FILE.....BINFN.....
outputs/fsh_mass.opt

OUTPUTS TRACK BINARY FILE.....BNTFN.....
outputs/fsh_btrk.opt

OUTPUTS CONSUMPTION BINARY FILE.....BCONF.....
outputs/consume.opt

APPENDIX D: Example of Migration File.

Atlantic menhaden moving on 4,000 cell Chesapeake Bay grid, 4/7/2009
Migratory Period
365.25

Time 0.00								
# Schools 3								
sid	event	box	size	# grps	gid	frac	gid	frac
1	Entry	72	6.23e+005	1	1	1.00		
2	Entry	72	3.81e+005	2	2	0.88	3	0.12
3	Entry	72	7.63e+005	1	4	1.00		
Time 0.25								
# Schools 2								
sid	event	box	size	# grps	gid	frac	gid	frac
2	Move	71	3.81e+005	2	2	0.88	3	0.12
3	Move	70	7.63e+005	1	4	1.00		
Time 0.50								
# Schools 3								
sid	event	box	size	# grps	gid	frac	gid	frac
1	Move	71	6.23e+005	1	1	1.00		
2	Move	72	3.81e+005	2	2	0.88	3	0.12
3	Move	69	7.63e+005	1	4	1.00		
Time 1.00								
# Schools 2								
sid	event	box	size	# grps	gid	frac	gid	frac
2	Exit	72	3.81e+005	2	2	0.88	3	0.12
3	Move	72	7.63e+005	1	4	1.00		
Time 1.25								
# Schools 2								
sid	event	box	size	# grps	gid	frac	gid	frac
1	Exit	72	6.23e+005	1	1	1.00		
3	Exit	72	7.63e+005	1	4	1.00		